

TROPHALLAXIS IN *POLISTES PALLIPES*.

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Wheeler,<sup>1</sup> in his paper on the origin of social habits, has given us some very interesting data on the mutualistic relationship between the mother or adult workers of insects and their larval brood. His data show that the relationship is clearly cooperative for ants, and he gathers from various sources similar data for other insects, and coins the word *trophallaxis* to encompass this phenomenon.

In the orphan nests of *Polistes pallipes* we have often seen behavior substantiating Dr. Wheeler's data, in a species where this type of behavior has not yet been recorded. The details more than substantiate the observations on other insects, because the behavior we record can be only purely instinctive, since the observations were made on orphan colonies, with the queen and older workers gone before these individuals had come to light, and hence there was no possibility for the habits to be learned from others.

On two occasions, I noticed that the foster-queen, just after feeding the larvæ, would stand on the nest and make a prolonged grating noise by rapidly vibrating her body, wings and legs. The noise was one which I had never before heard, and which is probably a signal to the larva, for immediately after this performance she would poke her head into each of the cells. I suspect that by this process she obtained a drink of saliva, but I have no proof of this except that her mouth parts were protruding and in motion when she withdrew her head. I suspected that she was going in for this purpose, and put my eye close enough to see when she came out of one cell; a large, glistening drop of liquid was in her mouth, which she soon swallowed. My

<sup>1</sup>Wheeler, W. M. A study of some ant larvæ, with a consideration of the origin and meaning of the social habit among insects. Proc. Am. Phil. Soc. 57: 293-343. 1918.

next move was to see if this liquid was used by the adult for food, or if it was collected, a drop at a time, and placed with the eggs in other new cells. Wheeler says that the females feed the young in exchange for the saliva which they emit at the time of feeding, but here we saw the saliva emitted long after they had been fed. I wonder if a worker can get a drink whenever it taps the head of a larva just as I can cause a large drop to come by teasing it with the head of a pin.

On one occasion two foster queens, after feeding the larvæ, went into the cells after sounding a noisy warning, evidently for the purpose of obtaining saliva. I watched very closely, and this time was able to see the method. The queen (so she will henceforth be called) stood on a nest with her head at the opening of a cell and her antennæ inside, probably touching the larva. Her head was then rapidly rammed or beaten against the wall of the cell; the whole body was in motion, seeming to actuate the head, and this rapid vibration of the head against the paper wall caused the strange sound. In one cell this drumming was repeated six times, and the duration of each round of it was one-fourth to one-half minute. After each trial the queen thrust her head into the cell, but obtained no saliva. I too could peer in by coming close beneath the nest, and there I found that after each serenade by the queen, the mouthparts of the larva were in agitated motion as if making effort, and a very small, glistening drop appeared on the mouth. In all probability the amount was not sufficient to satisfy the demands of the queen, for only after the sixth trial did she thrust her head far in and keep it there. These noises must have stimulated some others near by, for they too responded with a glistening drop in the mouth; into one of these cells she entered without the preliminary music. In most of the others, however, the warning was given but once. The queen's antennæ probably also acted as a stimulus, but her body always obstructed my view at that moment so I could not clearly see this. This first foster-queen had no exclusive patent rights on this scheme, for the second one used precisely the same methods.

This fact that the honey-dew, coming from the mouths of the larvæ, is lapped up and relished by the workers, is not new,

but has been recorded for other species of *Polistes* and other insects. Janet was able to prove in 1903 that the secretion is a product of the salivary or the spinning glands, and that it flows from an opening at the base of the labium. This act as I have observed it in orphan colonies must have been purely instinctive, since the individuals certainly had never been taught this trick, and the larvæ responded readily to the noisy tapping. They freely gave up this honey-dew also without associating this action with the noisy vibrations, for teasing the mouth-parts with a pin-head caused the same response. It is quite likely that, as Wheeler has so ably shown, this behavior is the cause of the beginning of the social habit. There is, however, another phase to the condition of trophallaxis, in the hypothesis that it might be absolutely necessary for the larva to rid itself of the substance that the workers so willingly take. In larvæ of this and various other species, there is no provision made for ridding the body of excretory products. During the period of feeding, the larvæ, being confined in close quarters, have no place for refuse. In most of the *Trypoxylon* wasps and in mud-daubing wasps, *Sceliphron cæmentarium*, this excretory material is passed from the body in one mass, just before pupation; it is spread and moulded to form a shell or cocoon covering the body. In *Polistes* cells, after the adults have emerged, there always remains up against the roof of the cell, a hard reddish mass of chalky material which is the sum total of the excretory products accumulated during the life of the larva. The thought comes to me, if the solid excretory matter leaves the body in that form what becomes of the liquid excreta? In the plant-lice, we know that the honey-dew, so much relished by the ants, is waste matter; why should that emitted by *P. pallipes* larvæ not likewise be excretory material? The only difference at once apparent is that one insect is relieved by delivery of this liquid from the posterior end, and the other by way of the anterior aperture of the body—a small digression when one considers how Nature disregards the method to gain her ends economically.

The question still remains, probably never to be solved, whether the *Polistes* nurse feeds the larvæ in order to get the honey-dew, or whether she relieves the larvæ of their moisture

to save their lives and has in time acquired a taste for it, but one can feel amply sure that the larva does not give this honey-dew because it loves the nurse or because it purposes to wheedle its keeper for a good meal. The larva at the slightest stimulus gives up its drop, perhaps only because it wants to rid itself of so much irritating material.